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Laboratoire des Reptiles et Amphibiens, Muséum national d'Histoire naturelle, 25 rue Cuvier, 75005 Paris, France. – Tel.: (33).(1).40.79.34.87. – Fax: (33).(1).40.79.34.88. – E-mail: ohler@mnhn.fr.

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Two new *Telmatobius* species (Leptodactylidae, Telmatobiinae) of Ancash, Peru

Antonio W. SALAS * & Ulrich SINSCH **

* Museo de Historia Natural, Universidad Ricardo Palma, Av. Benavides cdra. 54, Santiago de Surco, Lima, Peru

** Institut für Biologie, Universität Koblenz-Landau, Rheinau 1, 56075 Koblenz, Germany

The taxonomic status of two populations of telmatobiine frogs in the Peruvian department Ancash is evaluated using data from external morphology. The intrapopulational variation of 18 morphometric measures is compared with those of six telmatobiine species from adjacent regions: *Batrachophrynus brachydactylus, B. macrostomus, Telmatobius brevirostris, T. carrillae, T. jelskii* and *T. rimac*. The frogs inhabiting the Laguna Conococha and those of the Rio Sihuas are distinct from the already described species and from each other. They represent two new species of the genus *Telmatobius*. Diagnostic features of external morphology and skin histology are given to distinguish among the central Peruvian Telmatobiinae.

INTRODUCTION

The streams and lakes of the central and northern regions of the Peruvian Andes are inhabited by leptodactylid frogs of the genera *Telmatobius* Wiegmann, 1835 and *Batrachophrynus* Peters, 1873 (DUELLMAN, 1979; SINSCH, 1990; WIENS, 1993). *Batrachophrynus* is endemic to central Peru, whereas *Telmatobius* has a widespread distribution ranging from Ecuador in the north to Chile and Argentina in the south (CEI, 1986). The taxonomic status of populations of telmatobiine frogs is difficult to evaluate, if only based on external morphology, because shape and coloration are usually similar due to the adaptation to the mostly riparian habitats. The original descriptions and diagnoses of most species are inadequate and the taxonomic classification of populations often requires comparison with type material. In many taxa, multivariate statistics such as discriminant analyses are necessary to distinguish between intraspecific and interspecific variation of

morphometric measures (Wiens, 1993; Sinsch et al., 1995). In others, genetic markers such as allozyme loci are used to assess the specific status (Wiens, 1993). These approaches were recently used to evaluate the status of several populations inhabiting the Andean regions of the northern Peruvian departments of Amazonas, Cajamarca, La Libertad and Piura (Wiens, 1993) and of the central Peruvian departments of Ancash, Ayacucho, Cerro de Pasco, Huancavelica, Huanuco, Junin and Lima (Sinsch et al., 1995; Sinsch & Juraske, 1995). The known species of the north-Peruvian departments are *Telmatobius brevipes* Vellard, 1951, *T. ignavus* Barbour & Noble, 1920, *T. latirostris* Vellard, 1951, and the six species recently described by Wiens (1993), *T. atahualpai*, *T. colanensis*, *T. degener*, *T. necopinus*, *T. thompsoni* and *T. truebae*. The reassessment of the status of the central Peruvian populations led to the recognition of *Batrachophrynus brachydactylus* Peters, 1873, *B. macrostomus* Peters, 1873, *Telmatobius brevirostris* Vellard, 1955, *T. carrillae* Morales, 1988, *T. jelskii* (Peters, 1873) and *T. rimac* Schmidt, 1954.

Information on the Telmatobiinae inhabiting the department of Ancash are still scarce. The few populations which have been treated taxonomically have been assigned to three species of *Telmatobius*: *T. rimac* (Vellard, 1955; Morales, 1988*a*), *T. jelskii* (Morales, 1988*a*) and *T. carrillae* (Morales, 1988*b*; Salas, 1990). The most recent checklist of amphibian species of Peru (Rodríguez et al., 1993) recognizes only the occurrence of *T. carrillae* and *T. rimac* in Ancash. A thorough survey of the amphibians of this region during eight years (1986-1994) by the senior author revealed the existence of two populations of telmatobiine frogs which apparently differed in some characters of external morphology from these species and others known to inhabit the adjacent central Peruvian departments (Salas, unpublished data). These observations motivated the senior author to reevaluate the taxonomic assignment of telmatobiine frogs collected in Ancash and preserved in local collections. The morphometric analysis (using the classification criteria of Sinsch et al., 1995) of the specimens collected in the Rio Huaylas and assigned to *T. jelskii* by Morales (1988*a*) showed that they had been confounded with *T. rimac* (Salas, in preparation). In contrast, the populations of telmatobiine frogs collected in the Laguna Conococha and in the Rio Sihuas remained unidentified, though the first superficially resembles *Batrachophrynus brachydactylus*, and the second *Telmatobius carrillae*. Both populations differ in several aspects from all other species and also between each other.

The aims of this paper are to: (1) establish the distinction of the populations inhabiting the Laguna Conococha and the Rio Sihuas from the already described species of this region; (2) describe two new species; and (3) justify their inclusion in the genus *Telmatobius*.

Material and methods

The material examined included adult frogs pertaining to six previously known species (*Batrachophrynus brachydactylus*, N = 53; *B. macrostomus*, N = 13; *Telmatobius brevirostris*, N = 5; *T. carrillae*, N = 43; *T. jelskii*, N = 71; *T. rimac*, N = 42), and 25 unclassified specimens which were collected in the Laguna Conococha, Provincia Recuay,

Department of Ancash, Peru (13 adults, 2 subadults), and in the Rio Sihuas, Provincia Sihuas, Department of Ancash, Peru (10 adults), respectively. The geographical distribution of the collection sites are shown in figure 1. The detailed list of specimens of the 6 previously known species, with their localities and museum collections, was already published by SINSCH et al. (1995: 43-44, Appendix I). As for the 25 unclassified specimens, their detailed list is given below under the two newly described species. Institutional abbreviations are as follows: KU, Museum of Natural History, The University of Kansas, USA; MHNSM, formerly MHNJP, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; URP, Museo de Historia Natural, Universidad Ricardo Palma, Lima, Peru; ZFMK, Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

Standard morphometric measurements were recorded from all adult specimens to the nearest 0.1 mm with needle-tipped calipers, as in WIENS (1993) and SINSCH et al. (1995). Note that measurements of limbs refer to the portions of body containing the bones: (1) SVL, snout-vent length; (2) BH, height of body (at the pectoral girdle); (3) HWID, maximum width of head; (4) EYE, eye diameter; (5) IOD, interorbital distance; (6) ENOSE, eye-nostril distance (anterior margin of eye to posterior edge of naris); (7) ESNOUT, distance between the eye and the tip of the snout; (8) HUML, humerus length (upper forelimb); (9) RADL, radioulnar length (lower forelimb, elbow to distal edge of outer palmar tubercle); (10) HNDL, hand length (proximal edge of outer palmar tubercle to tip of third finger); (11) FG3L, length of the third finger; (12) FEML, femur length (thigh); (13) TIBL, tibia length (shank, knee to heel); (14) FOOTL, foot length (from union with tibia to the tip of fourth toe); (15) TOE1L, length of first toe; (16) TOE4L, length of fourth toe; (17) CIL, length of callus internus; (18) WEBL, maximum length of toe web between III and IV (from the middle of the web, i.e. lowest part, to the union of the toes).

Multivariate analyses were performed on $\log_{10}$-transformed data (BOOKSTEIN et al., 1985) and morphometric ratios. The empiric measurements were transformed to ratios (range: 0-1) by calculating measures relative to SVL (SINSCH et al., 1995). Moreover, two indices were used for further analysis: CIL/TOE1L and FEML/TIBL.

The first step of classification was to calculate the discriminant scores for the adult specimens from the Laguna Conococha and Rio Sihuas using the discriminant functions published by SINSCH et al. (1995), which distinguish among *Batrachophrynus brachydactylus*, *B. macrostomus*, *Telmatobius brevirostris*, *T. carrillae*, *T. culeus*, *T. jelskii* and *T. rimac*. The second step consisted in subjecting sets of the $\log_{10}$-transformed data to principal component analysis to explore the morphometric variability independent of taxonomic assignment. Data sets were: (1) *Batrachophrynus brachydactylus*, *B. macrostomus*, taxon from Rio Sihuas and taxon from Laguna Conococha; (2) *Telmatobius brevirostris*, *T. carrillae*, *T. jelskii*, *T. rimac*, taxon from Rio Sihuas and taxon from Laguna Conococha. Principal components (PC) are linear combinations of the measured variables, uncorrelated with each other and explaining the maximum amount of variation. The first principal component (PC1) of morphometric data generally describes differences in size, but size effects may be present in subsequent principal components (HUMPHRIES et al., 1981). Techniques such as shearing have been developed to correct PC2 and PC3 for possible size

effects (Bookstein et al., 1985), but they are controversial and size effects may still persist (Rohlf & Bookstein, 1987). Therefore, we present the uncorrected PC2 and PC3. The next step consisted in a stepwise canonical discriminant analysis to distinguish between the taxonomic groups delimited a priori. We used stepwise forward selection of variables (criterion to enter: $F = 4.0$) to minimize the number of variables needed for group distinction. The resulting discriminant functions (CAN: canonical variables) are linear combinations of those measured variables that maximize the differences between the groups. Discriminant functions were derived from the $\log_{10}$-transformed data. The final step of analysis was to look for diagnostic morphometric ratios which differ significantly among the known species and the taxa from Conococha and Sihuas. We applied a multiple range test using the Least Square method and a significance level of 1 %. All calculations were performed on a Pentium PC using the program package STATGRAPHICS Plus, version 1.4.

The descriptions of the new species follow the format of Trueb (1979) and Wiens (1993). The diagnosis only distinguishes among the species included in this paper. The formulae for toe webbing follow Savage & Heyer (1967) as modified by Myers & Duellman (1982).

Results and discussion

Classification with the discriminant functions which distinguish among the central Peruvian species

The morphometric features of the adult frogs which were collected in the Laguna Conococha and in the Rio Sihuas are listed in Tables I and II. The corresponding data for *Batrachophrynus brachydactylus*, *B. macrostomus*, *Telmatobius brevirostris*, *T. carrillae*, *T. jelskii* and *T. rimac* have been published by Sinsch et al. (1995: Tables I-II).

Eighteen $\log_{10}$-transformed morphometric characters were used to obtain discriminant functions which distinguish among the described telmatobiine species of central Peru (Sinsch et al., 1995: Tables III-IV). The first step of classification consisted in calculating the scores for the adult individuals of the Conococha and Sihuas samples using these discriminant functions. If the unclassified frogs are conspecific with any of the described central Peruvian species, we expect that the discriminant scores are completely or at least to a large amount within the known ranges of these species.

The discriminant scores based on the functions which distinguish among *Batrachophrynus brachydactylus*, *B. macrostomus*, *Telmatobius brevirostris* and *T. carrillae* are shown in figure 2. All scores of the specimens from Rio Sihuas are placed outside the variation of any of the known species with respect to CAN1 and CAN2. In contrast, the scores of the Conococha individuals completely overlap with the range of variation of *T. brevirostris*. However, the scores obtained using CAN3 distinguish both Conococha and Sihuas specimens from *T. brevirostris*. In a three-dimensional plot of these discriminant functions there is no overlap of the distributions obtained for the samples from Laguna

Conococha and from Rio Sihuas with that of *Batrachophrynus brachydactylus*, *B. macrostomus*, *Telmatobius brevirostris* or *T. carrillae*. In conclusion, the telmatobiine frogs of the unclassified populations remain unidentified and are probably not conspecific with any of these species.

The same analysis was done applying the discriminant functions which distinguish among *T. culeus*, *T. jelskii* and *T. rimac*. The distribution of scores obtained for the frogs of the two unclassified populations does not overlap with the range of *T. culeus*, but some scores are inside the ranges of *T. jelskii* and *T. rimac* (fig. 3). Nevertheless, most scores of both populations are outside the ranges of either *T. jelskii* or *T. rimac*, especially those of the frogs from Laguna Conococha. These results do not suggest that the unclassified frogs pertain to either species, but due to the slight overlap conspecificity cannot entirely be ruled out. However, the frogs of Rio Sihuas are not only morphometrically similar to *T. jelskii* and *T. rimac*, but also share the presence of yellow-orange patches on the ventral side of the thigh with these two species.

Only *T. rimac* is known to occur in Ancash, in three localities along the occidental cordillera (SALAS, in preparation), whereas the nearest locality of a *T. jelskii* population is situated more than 300 km south of the unclassified populations (VELLARD, 1955; SINSCH et al., 1995). The centres of distribution of *T. jelskii* are clearly the more southern departments of Ayacucho, Junin and Huancavelica. Considering our limited knowledge on the distribution of most Peruvian Telmatobiinae, the biographical argument against the conspecificity with *T. jelskii* is admittedly weak.

Finally, we have to consider the characters related to sexual maturity. A diagnostic character for *T. jelskii* among the central Peruvian Telmatobiinae is the presence of horny excrescences on the chest of reproductive males. This feature is not shared by the males collected in the Laguna Conococha and in the Rio Sihuas. The minimum size of the Conococha adults is about 67 mm SVL (Table I); two smaller individuals (54 mm and 57 mm SVL) were still sexually immature. At all localities and elevations so far known, *T. jelskii* and *T. rimac* reach maturity at a considerably smaller size: 47 mm and 42 mm SVL, respectively. In contrast, the size distribution of the Rio Sihuas frogs clearly falls within the range of these species.

In conclusion, the morphometric data indicate that the taxon inhabiting the Laguna Conococha is certainly not conspecific with any of the described central Peruvian species. The taxon occurring in the Rio Sihuas is certainly distinct from *Batrachophrynus brachydactylus*, *B. macrostomus*, *Telmatobius brevirostris*, *T. carrillae*, *T. jelskii* and *T. culeus*, but some individuals cannot be morphometrically distinguished from *T. rimac*.

MORPHOMETRIC DISTINCTION OF THE UNCLASSIFIED TAXA FROM THE CENTRAL PERUVIAN SPECIES

In the second step of classification, we applied principal component and discriminant analyses to distinguish the unidentified populations from described central Peruvian species. Analyses were performed on two data sets: (1) *Batrachophrynus brachydactylus*, *B. macrostomus* and the samples from Rio Sihuas and Laguna Conococha; (2) *Telmatobius*

brevirostris, *T. carrillae*, *T. jelskii*, *T. rimac* and the samples from Rio Sihuas and Laguna Conococha.

Generally, the interspecific differences in size (PC1) by far exceeded those in shape (PC2, PC3). The size effects on PC2 and PC3 appeared to be small, because shearing showed little effect. Discriminant analysis led to an optimal separation of species by combining differences in size and shape.

In the data set used to distinguish the Conococha and Sihuas taxa from the *Batrachophrynus* species, the first three principal components explained 95.4 % of the total variance. PC1 accounting for 88.9 % of total variance separates the large *B. macrostomus* from the smaller *B. brachydactylus* and the unidentified taxa. The plot of PC2 (3.9 % of total variance) and PC3 (2.6 % of total variance) scores shows that the scores of the similar-shaped *B. brachydactylus* and *B. macrostomus* form one completely overlapping group, and those of the Conococha and Sihuas taxa another group (fig. 4A). The slight overlap between the two groups is due to scores of the Conococha taxon, whereas the scores of Sihuas taxon vary outside the range of the *Batrachophrynus* species. A perfect separation of the four taxa – 100 % of the specimens correctly classified – was obtained by stepwise discriminant analysis (fig. 4B, Table III). The taxa are distinguished based on only four out of 18 variables: FG3L, HUML, RADL and TOE4L, i.e. parameters of limb morphology.

In the data set used to distinguish the Conococha and Sihuas taxa from the central Peruvian *Telmatobius* species, the first three principal components accounted for 84.4 % of the total variance. PC1 accounting for 71.4 % of total variance separates the small *T. carrillae* from the larger taxa. The plot of PC2 (8.1 % of total variance) and PC3 (4.9 % of total variance) scores shows a complete separation of Conococha taxon from *T. brevirostris*, *T. jelskii* and *T. rimac*, but a considerable overlap with *T. carrillae* and the Sihuas taxon (fig. 5A). The best separation of the six taxa was obtained by discriminant functions based on a set of 13 out of 18 variables (Table IV). As five discriminant functions are necessary to separate six taxa, a presentation in a single plot would require five dimensions. Therefore, we present, as an example, a plot of CAN1 versus CAN2 which distinguishes *T. carrillae* and *T. jelskii* from all other species (fig. 5B). Based on five discriminant functions, 94.3 % of all specimens were correctly classified. The erroneous classifications were: 1 out of 53 *T. carrillae* which was confounded with *T. rimac*; 5 out of 71 *T. jelskii* which were confounded with *T. brevirostris*, *T. rimac* and the Sihuas taxon, respectively; 5 out of 42 *T. rimac* which were confounded with *T. brevirostris* and *T. jelskii*, respectively. Thus, none of the unidentified specimens was confounded with a known taxon.

In conclusion, the analyses presented demonstrate that the two samples of unidentified telmatobiine frogs represent morphometrically well-defined taxa which can be distinguished without erroneous classification from the six sympatric *Batrachophrynus* and *Telmatobius* species, and from each other.

Taxonomic decisions and generic assignment

The taxa inhabiting the Laguna Conococha and the Rio Sihuas, respectively, possess unique characters that easily and consistantly separate them from the other central

Peruvian Telmatobiinae (external morphology: figs. 6-7; skin histology: HEIN, 1994; HEIN & SINSCH, 1995; SINSCH & HEIN, in preparation). Moreover, there is no indication that any of the unidentified taxa in the department Ancash is conspecific with the north Peruvian *Telmatobius* species which inhabit the Andes near the Huancabamba depression (WIENS, 1993; WIENS, personal communication; SALAS, unpublished observations). Therefore, we conclude that the telmatobiine frogs of the populations inhabiting the Laguna Conococha and the Rio Sihuas are members of new species.

The generic assignment of the new taxa to *Telmatobius* is based on the following considerations. In central Peru, the Telmatobiinae are represented by the genera *Telmatobius* and *Batrachophrynus*. There are two presumptive synapomorphies for the monophyly of *Telmatobius* (WIENS, 1993): frontoparietals fused posteriorly, and nuptial excrescences on finger I only. In contrast, evidence for the monophyly of *Batrachophrynus* is based on allozymes, and on diagnostic features such as the absence of maxillary and prevomerine teeth, and nuptial pads without horny excrescenses (PETERS, 1873; LYNCH, 1978; SINSCH & JURASKE, 1995). *Alsodes* is assumed to be the sister taxon of *Telmatobius* (LYNCH, 1978), though the only presumptive synapomorphy is the presence of an enlarged crista medialis on the humerus in males (WIENS, 1993). However, allozymes and skin morphology rather indicate that *Telmatobius* and *Batrachophrynus* are sister taxa (HEIN & SINSCH, 1995; SINSCH & JURASKE, 1995; SINSCH & HEIN, in preparation): (1) NEI's genetic distances between the species of these genera are low; (2) *Telmatobius* and *Batrachophrynus* share the presence of granular glands with small granules which are absent in *Alsodes* (*A. montanus*); (3) *Telmatobius* (except for *T. carrillae*) and *Alsodes* share the presence of granular glands with large granules, but granules and gland structure are very different in the two genera (SINSCH & HEIN, in preparation); (4) *Telmatobius* and *Batrachophrynus* share the absence of nuptial excrescences on finger II which are present in *Alsodes*. Analyzing the character states considered as diagnostic for the genera *Alsodes*, *Batrachophrynus* and *Telmatobius* in the two new taxa, we find: (1) horny nuptial excrescences are present only on finger I; (2) maxillary and premaxillary teeth are present; (3) two types of granular glands (small and large granules) are present. A conservative evaluation of these character states suggests a provisional inclusion of the new taxa in the genus *Telmatobius*. Further comparative studies on allozymes, osteological and histological characters are needed and in work to test the validity of this assignment.

ACCOUNT OF THE NEW SPECIES

Telmatobius hockingi sp. nov.

(figs. 8-9)

Holotype. — URP 116, adult male, from Rio Sihuas 5 km from Sihuas, Provincia Sihuas, Departamento Ancash, Peru, 2700 m altitude, 77°38′14″W 08°30′00″S, collected on 19 december 1992 by Antonio W. SALAS.

Paratypes. — URP 112-115 and 117-119, 3 males and 4 females; ZFMK 57260, 1 male; KU 220844, 1 female; all collected at the same site simultaneously with the holotype by Antonio W. SALAS.

Diagnosis. — (1) Premaxillary teeth present; (2) tympanum absent; (3) nuptial spines moderately small on the dorsal and ventral surfaces of the thumb; nuptial pads continuous with inner palmar tubercle; (4) dorsum brownish grey (in preservative) with small patches; (5) venter dark cream with diffuse grey; (6) forelimbs and hindlimbs always without ornamentation or transverse bars; (7) dorsal skin smooth; (8) snout-vent length in males to 52.5 mm, in females to 64.8 mm.

This species resembles in habitus the riparian *Telmatobius* (fig. 8). Confusion with the sympatric *Batrachophrynus* species is impossible due to the difference in adult size, the easily noticeable premaxillary teeth, and the presence of nuptial excrescences and of granular glands with large granules in the dorsal skin. Moreover, the morphometric ratios HWID/SVL and FG3L/SVL are diagnostic for the distinction of *T. hockingi* from *Batrachophrynus* (fig. 6). *T. hockingi* differs from *T. brevirostris*, *T. jelskii* and *T. rimac* by the ratio HUML/SVL, and from *T. carrillae* and the new species described below by the ratio FG3L/SVL (fig. 7). The yellow-orange patches on the ventral side of the thigh distinguish *T. hockingi* from *T. brevirostris*, *T. carrillae* and the new species described below.

Description. — Head slightly narrower than body; head wider than long: HLEN 88.3 % of HWID; head length 30.4 % of SVL; head width 34.4 % of SVL. Dorsal view of snout rounded, in lateral profile gently sloping (fig. 9A). Nostrils not protuberant, located at the extreme anterior terminus of snout, anterolaterally oriented. Canthus rostralis indistinct dorsally, in lateral profile short and elevated; loreal region concave. Eyes protuberant on top of head, eye diameter 29.3 % of head length. Tympanum absent, tympanic annulus conspicuous. Supratympanic fold present and well developed, extending from posterior corner of eyelid to the anteroventral insertion of forelimb. Maxillary and premaxillary teeth embedded in labial mucosa, fanglike and protruding, but easily noticeable when passing on top with finger tips. Dentigerous processes of vomer well developed, five times closer to choanae than to each other, located anterior to choanae; choanae about the same size and circular. Tongue rounded with slightly elevated lateral borders, posteriorly free. Vocal slits absent.

Robust, stout forelimbs. Dermal wrist fold present, but inconspicuous. Fingers uniform in diameter, long and slender; I and II separated due to well developed muscles at the palmar region of insertion. Relative length of fingers: III > IV > I > II (fig. 9B), tips of fingers round to spherical, palmar webbing absent. In males, large and raised nuptial pad covering the dorsal and lateral surface of thumb; nuptial spines, moderately large, conical, keratinized. Inner palmar tubercle oval, continuous with nuptial pad. Outer palmar tubercle oval and large, but smaller than the inner, located proximally on fingers II and III. Conspicuous, supernumerary tubercles close to the base of fingers I and II. Subarticular tubercle present proximally on each finger except III, smaller subarticular tubercles in the middle of each finger and distal ones in III and IV.

Robust, but slender hind limbs. Hind limb length (foot plus tibia) 41.5 % of SVL. Relative length of toes (fig. 9C): IV > III > V > II > I; webbing formula: I 1 – 2+ II 2– – 3 2/3 III 2+ – 3– IV 3– – 1 V; webbing diminishes gradually to form a lateral fringe along the edge of toe IV. Tips of toes spherical and of the same size as finger tips. Inner metatarsal tubercle small, oval and slightly raised; outer metatarsal tubercle

round, 1/3 length of inner. Small, round subarticular tubercles distributed on toes as follows: I(1), II(1), III(2), IV(3) and V(2). Tarsal fold extending to 1/3 length of tarsus, confluent with lateral fringe of toe I.

Dorsal, ventral and lateral skin smooth. Ventral skin covered with few and isolated, unconspicuous pustules. Cloacal opening dorsoventrally flattened.

Colour in life. — Dorsum yellowish orange with large irregular shaped black patches, venter creamy yellow with large yellow-orange patches in the pubic region; iris yellow.

Colour in preservative. — Dorsum and dorsal surfaces of limbs blue grey with large dark patches, venter and underside of limbs dull cream with scattered pale grey regions distributed over the whole area, underside of thighs with isolated or connected light patches.

Measurements (mm) of the holotype. — SVL 52.5; BH 14.2, HWID 18.1; EYE 4.7; IOD 12 2; ESNOUT 8.1; HUML 8.9; RADL 13.5; HNDL 12.3; FG3L 7.4; FEML 26.4; TIBL 24.9; FOOTL 40.9; TOE1L 5.6; TOE4L 27.0; CIL 2.6; WEBL 5.8.

Distribution. — *Telmatobius hockingi* is known only from the type locality and from Piscobamba, Ancash.

Ecology. — Frogs of the type series were collected during the day under rocks in a stream (Rio Sihuas) of strongly running water passing through an alder (*Alnus jorullensis*) forest. The stream is used for the irrigation of the adjacent agricultural areas. Sometimes, the stream dries, but small pools persist. These pools and moist soil below rocks are used by the frogs to survive the dry period.

Etymology. — The specific name (a noun in the genetive case) is a patronym for Pedro HOCKING of the Natural History Museum of the San Marcos University (MHNSM), Lima, in recognition for his important contributions to the knowledge of biodiversity of Peru.

Telmatobius mayoloi sp. nov.

(figs. 10-11)

Holotype. — URP 106, adult male, from the mouth of Rio Santa, 500 m from Lake Conococha, Provincia Recuay, Departamento Ancash, Peru, 4050 m altitude, ca. 77°17′50″W 10°06′25″S, collected on 29 december 1992 by Eladio Turya CASTILLO

Paratypes. — URP 103-105 and 107-111, 1 male, 6 females and 1 juvenile, MHNSM 7413 and 7419-7421, 1 male, 2 females and 1 juvenile, ZFMK 57259, 1 female; KU 220842, 1 female; all collected at the same site as the holotype by Antonio W. SALAS.

Diagnosis. — (1) Premaxillary teeth present, almost completely embedded in labial mucosa; (2) tympanum absent; (3) nuptial spines minute, on dorsal and ventral surface of the thumb; (4) dorsum blue grey (in preservative) with large dark blotches; (5) venter light grey (in preservative) with small black spots; (6) forelimbs and hindlimbs with transverse bars; (7) skin of dorsum smooth; (8) snout-vent length in males to 90.3 mm (MHNSM 7413), in females to 84.3 mm (ZFMK 57259).

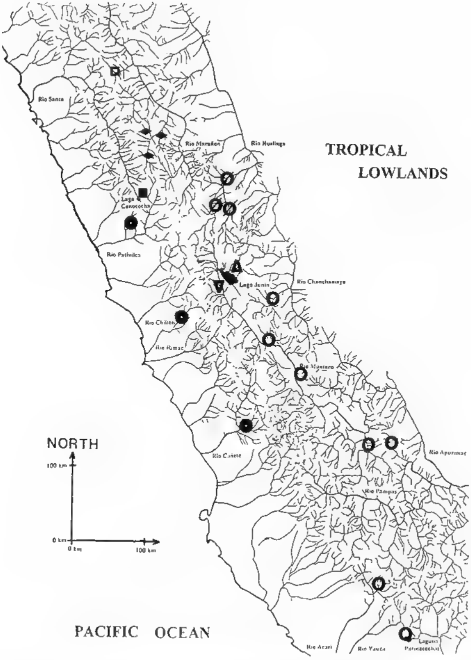


Fig 1. – Distribution of northern and central Peruvian telmatobiine populations. Inverted triangle, *Batrachophrynus brachydactylus*; triangle, *B. macrostomus*; ø, *Telmatobius brevirostris*; rhombus, *T. carrillae*; open square, *T. hockingi*, circle, *T. jelskii*; filled square, *T. mayoloi*; dots, *T. rimac*. Localities are approximated from distances by roads; multiple localities in close proximity are represented by a single symbol. The main Andean river systems and lakes are indicated.

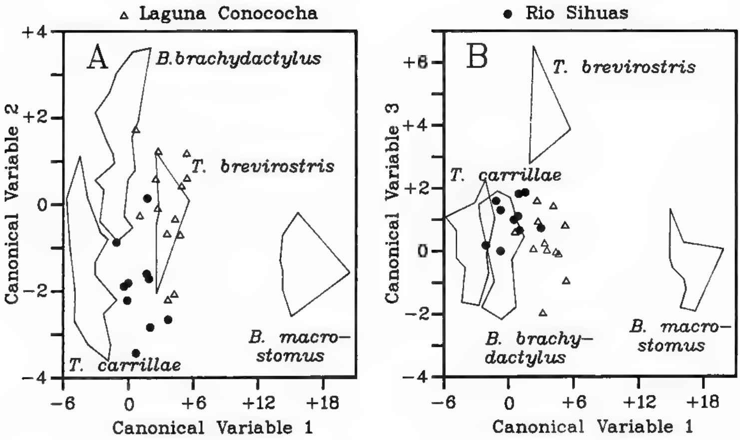


Fig. 2. — Plot of the discriminant function scores obtained for the populations from the Laguna Conococha and Rio Sihuas using the functions which distinguish among the ranges of morphometric variation of *Batrachophrynus brachydactylus*, *B. macrostomus*, *Telmatobius brevirostris* and *T. carrillae* (Sinsch et al., 1995) (A) CAN1 versus CAN2. (B) CAN1 versus CAN3.

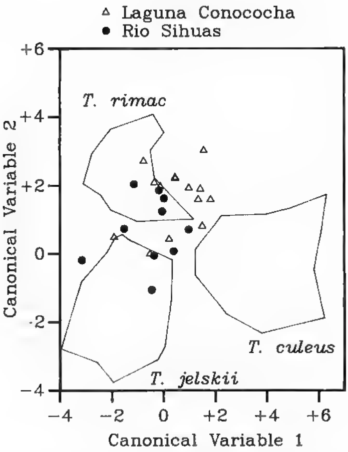


Fig. 3. – Plot of the discriminant function scores obtained for the populations from the Laguna Conococha and Rio Sihuas using the functions which distinguish among the ranges of morphometric variation of *Telmatobius culeus*, *T. jelskii* and *T. rimac* (Sinsch et al., 1995).

This species externally resembles *Batrachophrynus brachydactylus*, the only sympatric telmatobiine species similar in size and coloration (fig. 10). The morphometric ratio HWID/SVL is diagnostic for the distinction of *T. mayoloi* from *Batrachophrynus brachydactylus* (fig. 6). Moreover, the presence of embedded premaxillary teeth and nuptial excrescences as well as the rarely occurring granular glands with large granules in the dorsal skin distinguish *T. mayoloi* from *Batrachophrynus*. *T. mayoloi* differs from *T. brevirostris*, *T. jelskii* and *T. rimac* by the ratio HUML/SVL, and from *T. carrillae* and *T. hockingi* by the ratio FG3L/SVL (fig. 7).

Description. – Head width almost equal to body width; head width and length almost equal: HLEN 97 % of HWID, head length 34 % of SVL; head width 35 % of SVL. Dorsal view of snout rounded, in lateral profile similar to *T. atahualpai* (fig. 11A). Nostrils not

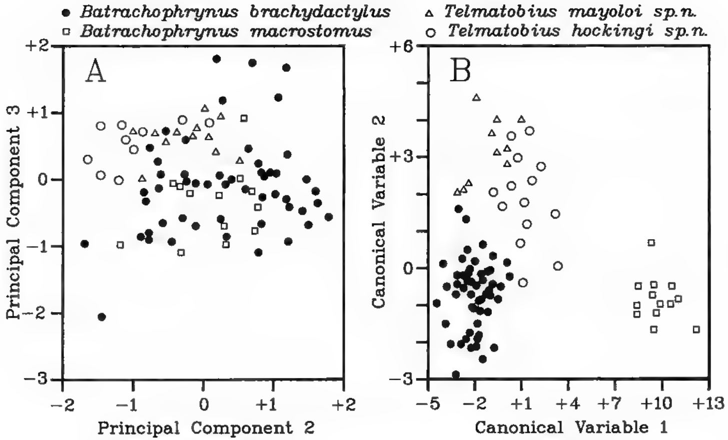


Fig. 4 – Plot of (A) principal component scores and (B) discriminant function scores of *Batrachophrynus brachydactylus*, *B. macrostomus*, *T. hockingi* and *T. mayoloi*. Discriminant functions (1-3) and classification success are given in Table III.

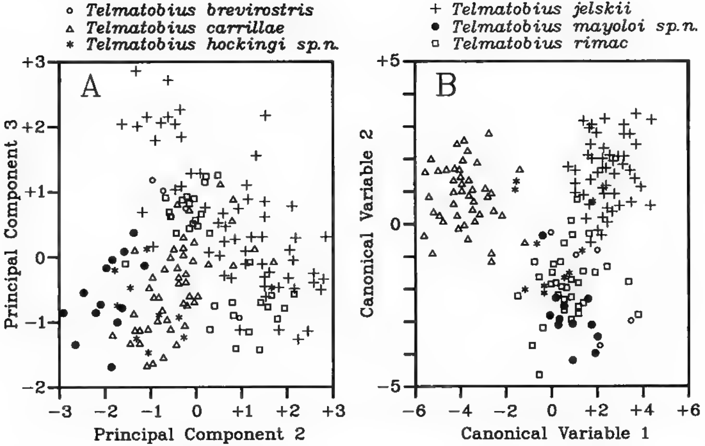


Fig. 5. — Plot of (A) principal component scores and (B) discriminant function scores of *Telmatobius brevirostris*, *T. carrillae*, *T. hockingi*, *T. jelskii*, *T. mayoloi* and *T. rimac*. Discriminant functions (1-5) and classification success are given in Table IV.

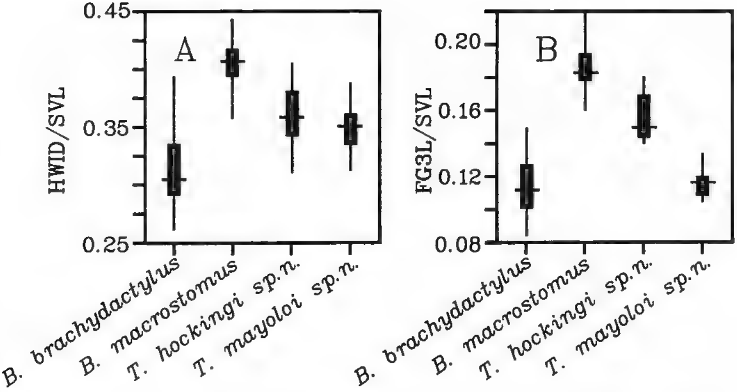


Fig. 6. — Box- and whisker-plot of morphometric ratios which permit the distinction among the *Batrachophrynus* species, *T. hockingi* and *T. mayoloi* (multiple range test, LSD-method, $P < 0.01$). (A) HWID/SVL: *B. macrostomus* > *T. mayoloi* = *T. hockingi* > *B. brachydactylus*. (B) FG3L/SVL: *B. macrostomus* > *T. hockingi* > *B. brachydactylus* = *T. mayoloi*.

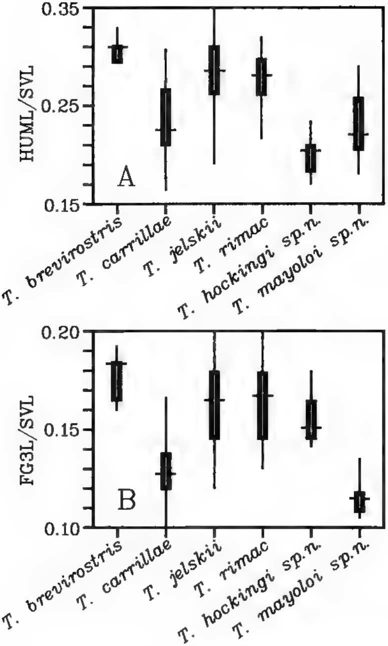


Fig. 7. – Box- and whisker-plot of morphometric ratios which permit the distinction among the known central Peruvian *Telmatobius* species, *T. hockingi* and *T. mayoloi* (multiple range test, LSD-method, $P < 0.01$). (A) HUML/SVL: *T. brevirostris* = *T. jelskii* = *T. rimac* > *T. carrillae* = *T. mayoloi* > *T. hockingi*. (B) FG3L/SVL: *T. brevirostris* > *T. jelskii* = *T. rimac* = *T. hockingi* > *T. carrillae* = *T. mayoloi*.



FIG. 8. — Photograph of a male *Telmatobius hockingi*

protuberant, located at the anterior terminus of snout. Canthus rostralis indistinct dorsally, in lateral profile short and elevated. Eyes not protuberant on top of head, eye diameter 27 % of head length. Tympanum absent, tympanic annulus inconspicuous Supratympanic fold present, extending from posterior corner of eyelid to insertion of forelimb. Maxillary and premaxillary teeth embedded in labial mucosa, slightly protruding, but almost unnoticeable when passing on top with finger tips. Well developed vertical fold posterior to corner of jaw, extending below supratympanic fold to throat. Dentigerous processes of vomer large and well developed, three times closer to choanae than to each other, located slightly anterior to choanae; choanae small and oval. Tongue large and rounded, attached through its complete length. Vocal slits absent.

Robust forelimbs, triangular shaped in cross section. Dermal wrist fold conspicuous, but weakly developed. Relative length of fingers: III > IV > II > I (fig. 11B), tips of fingers bluntly pointed, palmar webbing absent, lateral fringes absent. In males, inner palmar tubercle large and oval, continuous with nuptial pad. Outer palmar tubercle elliptical, about 2/3 of size of the inner. One large subarticular tubercle present proximally on each finger, smaller subarticular tubercles present along the longitudinal axis of each finger. In males, densely packed nuptial spines forming plush-like pads, extending on dorsal, medial ventral surface of thumb.

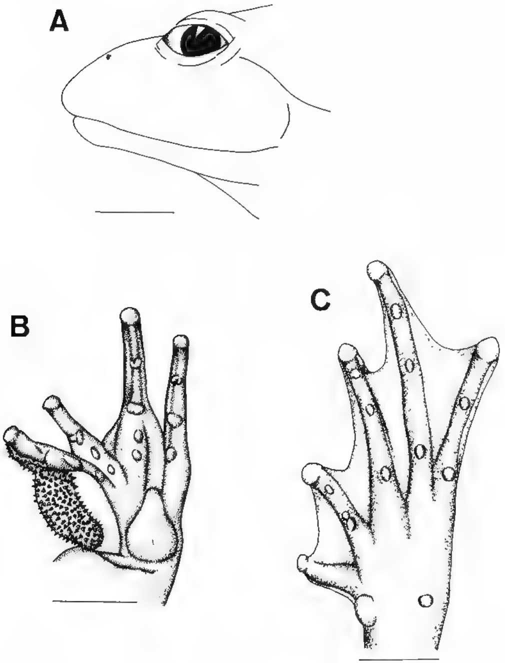


Fig 9 – Morphological details of male holotype URP 123 of *Telmatobius hockingi* (A) Lateral view of head. (B) Palmar view of right hand. (C) Plantar view of left foot. Scales = 5 mm



Fig. 10. — Photograph of a male *Telmatobius mayoloi.*

Stout hind limbs, dorsoventrally flattened; thighs with bagginess as in the lake-dwelling *B. macrostomus* and *T. culeus*. Hind limb length (foot plus tibia) 47.9 % of SVL. Relative length of toes (fig. 11C): IV > V > III > II > I; webbing formula: I 1 2/3 — 2+ II 1 1/3 — 3— III 2+ 3 1/3 IV 3 1/3 — 1 2/3 V; webbing diminishes gradually to form lateral fringes along the edges of toes II, III, IV and V. Tips of toes spherical in I, II and III, more pointed in IV and V. Inner metatarsal tubercle ovally elongated, raised; outer metatarsal tubercle equally shaped and elevated as inner, but only 2/3 in size. Small, round subarticular tubercles distributed on toes as follows: I (1), II (1), III (2), IV (3) and V (2). Tarsal fold extending to about 50 % of length of tarsus, confluent with lateral fringe of toe I.

Dorsal, ventral and lateral skin usually smooth Ventral skin covered with few and isolated, inconspicuous pustules. Cloacal opening hidden due to the bagginess of skin.

Colour in life. — Dorsum pale brown with orange tone, frequently covered with irregular shaped black blotches which often contain clear spots, forelimbs and hindlimbs with transverse black bars and clear spots as on the dorsum; venter creamy yellow with orange tone and black spots; iris orange with black reticulations.

Colour in preservative. — Dorsum grey with large, irregular shaped blotches; venter light grey with isolated black dots, forelimbs and hindlimbs with transverse bars.

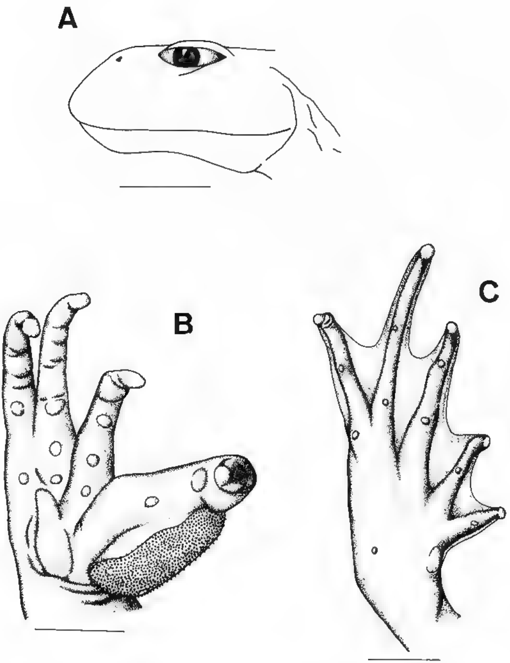


Fig. 11. — Morphological details of male holotype URP 111 of *Telmatobius mayoloi*. (A) Lateral view of head. (B) Palmar view of right hand. (C) Plantar view of left foot. Scales = 5 mm.

Table I. - Morphometric data for *Telmatobius mayoloi* and *T. hockingi*. The first line is mean ± 1 SD; the second line is range. All values are in millimeters; see text for abbreviations of variables.

Character	*Telmatobius mayoloi*		*Telmatobius hockingi*	
	Males N = 3	Females N = 10	Males N = 5	Females N = 5
SVL	78.5± 11.6 67.2 - 90.3	76.3 ± 5.7 69.7 - 84.3	47.7 ± 4.8 42.2 - 52.5	60.1 ± 4.2 53.2 - 64.8
BH	17.8 ± 2.7 15.1 - 20.4	17.0 ± 2.2 14.6 - 21.3	13.9 ± 0.9 12.9 - 15.2	16.6 ± 0.7 15.5 - 17.3
HWID	27.9 ± 4.2 23.6 - 32.0	26.8 ± 3.2 23.4 - 31.8	17.0 ± 0.8 16.2 - 18.1	21.9 ± 1.4 19.8 - 23.7
EYE	6.1 ± 1.0 5.2 - 7.1	5.7 ± 0.4 5.1 - 6.5	4.4 ± 0.6 3.9 - 5.3	4.9 ± 0.4 4.6 - 5.6
IOD	17.5 ± 2.4 15.3 - 20.0	17.6 ± 1.2 15.8 - 19.4	12.1 ± 0.8 11.1 - 13.0	14.2 ± 0.7 13.4 - 15.4
ENOSE	11.3 ± 1.2 10.1 - 12.5	10.6 ± 0.6 9.8 - 11.6	7.6 ± 0.5 7.0 - 8.3	8.8 ± 0.4 8.4 - 9.3
ESNOUT	16.3 ± 2.2 14.1 - 18.5	15.2 ± 1.0 13.5 - 16.7	10.9 ± 1.3 9.1 - 12.6	12.7 ± 0.5 11.9 - 13.3
HUML	19.2 ± 5.8 15.1 - 25.9	17.2 ± 3.1 12.8 - 22.1	9.9 ± 0.6 8.9 - 10.5	11.5 ± 0.7 10.7 - 12.3
RADL	16.7 ± 2.7 13.6 - 18.9	18.6 ± 2.6 14.7 - 23.1	11.8 ± 1.0 11.2 - 13.5	14.8 ± 0.6 13.8 - 15.5
HNDL	15.3 ± 4.1 11.3 - 19.4	15.6 ± 2.6 11.7 - 19.7	11.8 ± 1.3 10.5 - 13.8	14.2 ± 1.7 12.7 - 16.9
FG3L	9.2 ± 1.5 7.8 - 10.8	8.8 ± 1.2 7.3 - 11.5	8.2 ± 2.7 6.5 - 13.0	9.4 ± 1.3 8.6 - 11.6
FEML	35.8 ± 4.6 31.2 - 40.3	34.8 ± 5.3 26.8 - 43.4	23.2 ± 1.9 21.7 - 26.4	28.6 ± 1.0 27.8 - 30.2
TIBL	35.8 ± 4.8 31.4 - 40.9	34.4 ± 4.7 25.4 - 41.4	22.4 ± 1.6 21.3 - 24.9	27.5 ± 1.0 26.5 - 29.0
FOOTL	57.3 ± 7.8 49.9 - 65.5	54.1 ± 6.2 44.2 - 66.0	35.7 ± 3.1 33.0 - 40.9	44.4 ± 2.4 41.6 - 47.1
TOE1L	8.1 ± 1.4 6.6 - 9.3	7.8 ± 0.7 6.3 - 8.6	5.0 ± 0.5 4.3 - 5.6	6.5 ± 0.4 6.1 - 7.0
TOE4L	38.2 ± 6.2 32.3 - 44.6	35.4 ± 4.1 28.2 - 42.6	23.2 ± 2.4 21.1 - 17.0	28.8 ± 1.5 26.9 - 30.9
CIL	3.4 ± 0.8 2.6 - 4.2	3.2 ± 0.5 2.3 - 3.9	2.7 ± 0.4 2.1 - 3.0	3.2 ± 0.4 2.7 - 3.7
WEBL	11.2 ± 1.7 9.5 - 12.8	10.2 ± 2.7 6.7 - 15.7	7.7 ± 2.8 5.3 - 12.2	8.0 ± 1.8 6.0 - 10.6

Table II. - Ratios of morphometric data for *Telmatobius mayoloi* and *T. hockingi*. Data are given as mean ± 1 SD. See text for abbreviations of variables.

Ratio	*Telmatobius mayoloi* N = 13	*Telmatobius hockingi* N = 10
BH/SVL	0.224 ± 0.023	0.287 ± 0.035
HWID/SVL	0 351 ± 0.020	0.361 ± 0.026
EYE/SVL	0 076 ± 0.006	0.087 ± 0.007
IOD/SVL	0.228 ± 0.009	0.246 ± 0.016
ENOSE/SVL	0.141 ± 0.005	0.154 ± 0.010
ESNOUT/SVL	0.201 ± 0.012	0.221 ± 0.014
HUML/SVL	0.228 ± 0.033	0.201 ± 0.020
RADL/SVL	0.237 ± 0.035	0.248 ± 0.016
HNDL/SVL	0.202 ± 0.031	0.242 ± 0.019
FG3L/SVL	0.116 ± 0.010	0.164 ± 0.034
FEML/SVL	0.456 ± 0.044	0.484 ± 0.039
TIBL/SVL	0.451 ± 0.033	0.467 ± 0.026
FOOTL/SVL	0.713 ± 0.041	0.747 ± 0.035
TOE1L/SVL	0.102 ± 0.007	0.107 ± 0.009
TOE4L/SVL	0.468 ± 0.030	0.484 ± 0.020
CIL/SVL	0.042 ± 0.007	0.054 ± 0.008
WEBL/SVL	0.135 ± 0.027	0.147 ± 0.040
FEM/TIBL	1.010 ± 0.068	1.037 ± 0.041
CIL/TOE1L	0.416 ± 0.074	0.516 ± 0.093

Measurements (mm) of the holotype. – SVL 67.2; BH 15.1; HWID 23.6; EYE 5.2; IOD 15.3; ESNOUT 14.1; HUML 15.1; RADL 17.5; HNDL 11.3; FG3L 7.8; FEML 31.2; TIBL 31.4; FOOTL 49.9; TOE1L 6.6; TOE4L 32.3; CIL 3.3; WEBL 9.5.

Distribution. – *Telmatobius mayoloi* is known only from the type locality.

Ecology. – During the day frogs were found under rocks and among submerged plants within the mouth of the Rio Santa. Between 11 00 and 12.00 h, some individuals were observed swimming slowly in river parts with little current. Specimens were never seen outside the water. This species occurs in the Puna. Tadpoles have been found over the year in river pools and will be described in detail elsewhere.

Etymology. – The specific name (a noun in the genetive case) is a patronym for Antuñez de Mayolo, a renowned engineer native from Ancash.

Remarks. – Four of the specimens examined (URP 103-104 and 109, KU 220842) are large gravid females in an externally visible advanced state of egg development. The shape of gravid females is almost ovoid, whereas the shape of non-gravid females and males is slender and spindle-like. The head of the largest female is broad and similar-shaped as in *B. macrostomus*. The thumbs of the reproductive males show well-developed nuptial pads with minute, densely packed spines (fig. 11B). The two smallest individuals

Table III. - Discriminant functions to distinguish among *Batrachophrynus macrostomus*, *B. brachydactylus*, *Telmatobius hockingi* and *T. mayoloi* based on a stepwise discriminant analysis (procedure: forward selection) using 18 $\log_{10}$ transformed morphometric characters.

A. Statistical significance

Eigenvalue	Canonical correlation	Wilks Lambda	Chi-Squared	Degrees of Freedom	P
19 00	0.975	0.0093	392.5	12	< 0.00001
2.14	0.825	0.1869	140.9	6	< 0.00001
0 71	0.643	0.5863	44.8	2	< 0.00001

B. Unstandardized discriminant function coefficients

Character ($\log_{10}$)	Coefficients of CAN1	Coefficients of CAN2	Coefficients of CAN3
HUML	4.80	-18.27	-0.87
RADL	8 93	6.40	-1.13
FG3L	9.70	2.28	16.85
TOE4L	-0.92	11 65	-21 28
Constant	-23.83	-4.44	17.92

C. Classification success

	Predicted group			
Actual group	*B. brachydactylus*	*B. macrostomus*	*T. hockingi*	*T. mayoloi*
B. brachydactylus	53 (100%)	-	-	-
B. macrostomus	-	13 (100%)	-	-
T. hockingi	-	-	10 (100%)	-
T. mayoloi	-	-	-	13 (100%)

D. Group centroids

Species	CAN1	CAN 2	CAN3
B. brachydactylus	-2 47	-0.83	0 05
B. macrostomus	9.86	-0.77	0 36
T. hockingi	-1.15	3.09	1 46
T. mayoloi	1.07	1.79	-1.69

Table IV. - Discriminant functions to distinguish among *Telmatobius brevirostris*, *T. carrillae*, *T. hockingi*, *T. jelskii*, *T. mayoloi* and *T. rimac* based on a stepwise discriminant analysis (procedure: forward selection) using 18 $\log_{10}$ transformed morphometric characters.

A. Statistical significance

Eigenvalue	Canonical correlation	Wilks Lambda	Chi-Squared	Degrees of Freedom	P
6.98	0.935	0.0074	899.8	65	< 0.00001
2.23	0.831	0.0592	518.8	48	< 0.00001
1.24	0.744	0.1910	303.8	33	< 0.00001
0.75	0.654	0.4282	155.6	20	< 0.00001
0.33	0.501	0.7488	53.1	9	< 0.00001

B. Unstandardized discriminant function coefficients

Character ($\log_{10}$)	Coefficients of CAN1	Coefficients of CAN2	Coefficients of CAN3	Coefficients of CAN4	Coefficients of CAN5
SVL	-22.97	13.63	-17.21	-7.29	14.31
BH	-2.45	0.25	1.12	15.63	5.70
HWID	17.71	9.77	-7.71	-2.42	-11.60
EYE	-64.30	9.49	-1.13	13.69	76.91
IOD	103.47	-24.03	9.64	-22.62	-113.66
ESNOUT	20.77	8.78	15.76	8.15	-2.00
HUML	6.49	6.75	-2.23	-4.28	12.12
RADL	2.37	0.50	-11.28	7.70	-2.43
FG3L	8.77	5.51	6.90	8.02	-3.93
TIBL	-8.95	-23.58	-2.28	-8.86	6.28
TOE1L	-4.00	-15.26	4.33	0.05	-2.45
CIL	-3.06	-3.05	2.30	5.47	3.68
WEBL	-1.00	1.07	-1.99	-5.65	-4.67
Constant	58.94	-6.23	32.74	-1.40	-80.43

C. Classification success

Actual group	Predicted group					
	T. brevirostris	*T. carrillae*	*T. hockingi*	*T. jelskii*	*T. mayoloi*	*T. rimac*
T. brevirostris	5 (100%)	-	-	-	-	-
T. carrillae	-	52 (98%)	-	-	-	1 (2%)
T. hockingi	-	-	10 (100%)	-	-	-
T. jelskii	1 (1%)	-	2 (3%)	66 (93%)	-	2 (3%)
T. mayoloi	-	-	-	-	13 (100%)	-
T. rimac	2 (5%)	-	-	3 (7%)	-	37 (88%)

D. Group centroids

Species	CAN1	CAN2	CAN3	CAN4	CAN5
T. brevirostris	1.65	-1.72	1.24	3.05	2.67
T. carrillae	-4.05	0.63	-0.04	-0.09	0.11
T. hockingi	-0.19	-0.86	-0.25	2.74	-1.15
T. jelskii	2.37	1.37	-0.14	-0.10	0.01
T. mayoloi	0.76	-2.73	-3.46	-0.43	0.24
T. rimac	0.72	-1.86	1.27	-0.61	-0.17

(SVL 54.2 mm and 57.0 mm) without external sexual characters are considered as subadult juveniles.

RESUMEN

Se evalúa la situación taxonómica de dos poblaciones de ranas Telmatobiinae del Departamento de Ancash, Perú, mediante la comparación de la variación intrapoblacional de 18 de sus medidas morfométricas con las de seis especies de telmatobínidos de regiones adyacentes: *Batrachophrynus brachydactylus*, *B. macrostomus*, *Telmatobius brevirostris*, *T. carrillae*, *T jelskii* y *T. rimac*. Las ranas, que habitan la Laguna Conococha y el Rio Sihuas, no son miembros de las otras especies de la región. Las dos poblaciones representan dos especies nuevas del género *Telmatobius*: *T. hockingi* y *T. mayoloi*. Se presenta caracteres diagnosticos de la morfología externa y de histología de la piel para distinguir entre los Telmatobiinae del Perú central.

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A contribution to the ecological genetics of frogs: age structure and frequency of striped specimens in some Caucasian populations of the *Rana macrocnemis* complex

David N. TARKHNISHVILI & Ramaz K. GOKHELASHVILI

Group of Population Ecology, Department of Biology, Tbilisi State University, 380030, Chavchavadze avenue 1, Georgia

Four populations of Caucasian brown frogs (*Rana macrocnemis*) from different elevations and different mountain systems (Great and Minor Caucasus) were studied. In populations from the Minor Caucasus, the percentage of striped frogs increases with elevation, but not in the Great Caucasus. At the same time, age at sexual maturity in Caucasus Minor populations does not differ between forest and subalpine populations. It is suggested that in this region the increasing proportion of genetically striped frogs is the main adaptation preventing a decrease of reproductive potential with elevation. In the brown frogs metapopulation inhabiting the Great Caucasus, such a mechanism is absent.

INTRODUCTION

Specimens with a light mid-dorsal stripe (phenotype "striata") are found in populations of many anuran species. The inheritance of this character has been studied in several ranid species. Various authors have examined progeny produced as a result of crossings between striped and unstriped frogs collected from populations with different frequencies of the striped phenotype. A bright mid-dorsal stripe has been shown to be determined by a simple dominant gene in *Rana limnocharis* (MORIWAKI, 1953), *R. ridibunda* (BERGER & SMIELOWSKI), *R. sylvatica* (BROWDER et al., 1966) and *R. arvalis* (SHCHUPAK, 1977; SHCHUPAK & ISHCHENKO, 1981), though it has also been found that isolated striped specimens may appear even among offspring of unstriped parents of *R. limnocharis* (MORIWAKI, 1953) and *R. macrocnemis* (TARKHNISHVILI & MAMRADZE, 1989; TARKHNISHVILI, 1995). The most plausible reason for this appears to be the existence of phenocopies.

At the same time, the proportions of striped specimens in populations of some frog species display clinal variations, following climatic and landscape features. For example, the proportion of striped *R. sylvatica* in North America generally increases towards the west and north (FISHBECK & UNDERHILL, 1971; SCHUELLER & COOK, 1980). STUGREN

(1966) has shown that the proportion of striped specimens in populations of *R. arvalis* increases in an eastern direction; at the same time, northern populations of *R. limnocharis* in Japan are characterized by a reduced proportion of striped frogs (Moriwaki, 1953).

Previous authors have connected clinal changes in the proportion of different colour morphs with genetic-stochastic processes (e g. Stugren, 1966) or their adaptive importance (e.g. Merrell, 1969, 1973; Nevo, 1973; Dapkus, 1976; Ishchenko, 1978). In particular, for different colour morphs of the hylid *Acris crepitans* (the best studied species in this respect), the hypothesis about the direct adaptive value of different colour morphs (for escaping predation) competes with the hypothesis proposing a correlation of these morphs with important physiological characteristics, i.e. thermotolerance and desiccation resistance (Nevo, 1973); however, neither of these hypotheses has been supported experimentally (Gray, 1977, 1978). A similar situation is observed for a light mid-dorsal stripe in brown frogs. e.g. for *R. sylvatica*, Schueller & Cook (1980) suggest an advantage of striped specimens in open areas with the cryptic character of this pattern. Conversely, Ishchenko (1978) explains differences in the proportion of striped frogs between different populations of *R. arvalis* on the basis of physiological differences between different morphs. Schwarz & Ishchenko (1968), who compared striped and unstriped froglets emerging from the same breeding site, have shown that striped froglets have a relatively large liver, in comparison with unstriped ones, and that their weight increases more rapidly. L. Dobrinsky (see Ishchenko, 1978), who used an optic-acoustic gasoanalyser, demonstrated that metabolic exchange of striped froglets of *R. arvalis* is especially high: they excrete up to twice as much CO_2 per gram of body mass than unstriped ones. Tadpoles of striped *R. arvalis* need more time for completing metamorphosis (Ishchenko & Shchupak, 1974) but, after metamorphosis, their growth is more rapid than that of unstriped froglets, as shown by repeated measures of froglets with and without stripes, after their emergence from the breeding pond (Ishchenko, 1978). Vershinin (1987) has shown that in demes of *R. arvalis* where striped frogs predominate, froglets grow faster.

An interesting case of polymorphism is observed in populations of Caucasian brown frogs (*Rana macrocnemis* complex). Different forms of brown frogs inhabit the Caucasian Isthmus, Anatolia and mountain plateaus of the Middle East. The most widespread ones, *R. macrocnemis* and *R camerani*, represent closely related taxa included in the *Rana (Rana) temporaria* group (Dubois, 1992). The taxonomic status of these forms is not very clear. Some authors (e.g. Mensi et al., 1992) accept separate specific status of these frogs, while demonstrating their close relations. Baran and his co-authors (Baran, 1969; Baran & Atatur, 1986) demonstrated the presence of numerous populations with intermediate characters, representing a probable hybrid zone between the two species. Ishchenko & Pyastolova (1973) obtained hybrids from parents caught in typical "*macrocnemis*" and "*camerani*" populations; their viability, at least before and shortly after metamorphosis, was not lower than in control groups. Ishchenko (1978, 1987) found no consistent morphometric or coloration characters differentiating these two forms. He showed that the multidimensional distance (based on 20 morphometric indices) between separate populations of "*R macrocnemis*" and "*R. camerani*" in some cases exceeds the distance between populations composed of the two different forms. He concluded that subdivision of Caucasian brown frogs into two species is artificial.

At the same time, two forms of Caucasian brown frogs differ in the extent of altitudinal variation of some characters, in particular the proportion of striped specimens. Traditionally, one of the typical characters separating *R. camerani* from *R. macrocnemis* is a light mid-dorsal stripe (TERENTYEV & CHERNOV, 1940; BARAN, 1969). In frogs inhabiting Caucasus Minor, the proportion of striped specimens rapidly increases with elevation and reaches 80 % in the subalpine belt. This is not observed in the Great Caucasus, though some increase (up to 8 %) in the proportion of striped frogs with elevation can be observed in North Caucasus; in these specimens the stripe is poorly expressed (ISHCHENKO & PYASTOLOVA, 1973).

An increase in the percentage of specimens with a bright stripe at high elevations is clearly expressed in the region of the Trialeti Mountain Ridge (Georgia), bordering the north mountain plateaus of Caucasus Minor. Only a few striped specimens are found in the lowlands and foothills, although they predominate in the subalpine belt, in spite of the short distance between forest and subalpine populations and the very probable inter-population migrations: specimens which had been marked in the forest populations during the breeding period were sometimes caught later near the upper limit of the forest belt (our data), and, thus, the distance between populations does not exceed ranges of individual migrations. There are no barriers preventing interbreeding between frogs inhabiting foothill and subalpine populations. According to our long-term observations, in any population inhabiting the ridge a wide spectrum of phenotypes is found, from typical "*camerani*" with a bright stripe, relatively short legs and sharp snout, to typical "*macrocnemis*", and pair formation among these two forms appears to be totally random. In such conditions, the altitudinal differences we have described must presumably be the result of strong selection favouring striped specimens in the mountains.

The reproductive success of an animal depends on its fecundity, mortality at different stages of its life cycle and the period between successive generations (BEGON et al., 1986). Fecundity, reflected in the number of eggs per clutch, depends directly on body size. Differential mortality of different phenotypes can be estimated from changes in their proportions in consecutive age classes (ISHCHENKO, 1978). The period between generations can be estimated by studying the age distribution of adult animals. In connection with the data on the different growth rates of striped and unstriped frogs, a comparative analysis of the length of generation appears to be especially interesting. We studied the age distribution of five populations of *R. macrocnemis* inhabiting localities at different elevations and including different proportions of striped specimens.

MATERIAL AND METHODS

With the exception of frogs from Borjomi Canyon, animals were collected mainly during the period April to July, 1993 and 1994, from the following localities (fig. 1, Table I).

(1) Borjomi Canyon, western foothills of the Trialeti Mountain Ridge, northern slope. Forested canyon of the river Nedzura. Elevation 900-1100 m. Annual precipitation 1000-1200 mm (VLADIMIROV et al., 1991). Winter mild and wet. Period of activity for amphibians about six months, from the beginning of April to the beginning of October.

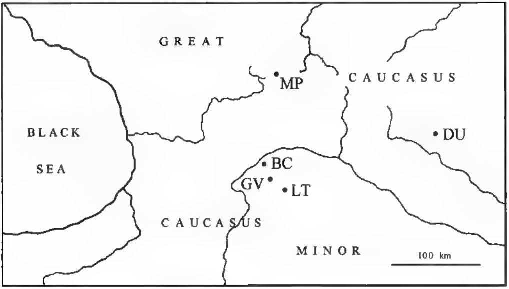


Fig. 1. — Map of Georgia, with indication of studied localities. BC, Borjomi Canyon; GV, Gujareti Village; LT, Lake Tabatskuri; MP, Mamisoni Pass, DU, Duruji Upstreams.

Total number of studied specimens, during two reproductive seasons (1992-1993), 138 adults: 106 males and 32 females.

(2) Gujareti Village. Western part of the Trialeti Ridge, northern slope. Subalpine meadows. Elevation 1900 m. Annual precipitation 800-1000 mm. Winter cold and dry. Period of activity for amphibians about four months, from the beginning of May to the beginning of September. Total number of studied specimens 47: 13 adult males, 6 adult female, 28 yearlings (body length 20-45 mm).

(3) Lake Tabatskuri, southern slopes of Trialeti Ridge, north-west of Javakheti Plateau, Caucasus Minor. Mountain steppe. Elevation 2000 m. Annual precipitation 1000 mm. Winter cold and dry. Period of activity for amphibians four months, from early May to early September Total number of studied specimens 63: 27 adult males, 13 adult females, 23 juveniles.

(4) Upstreams of the river Duruji, southern slopes of the eastern part of the Great Caucasus Mountain Ridge, in Kvareli District of Georgia. Subalpine meadows on the upper edge of the forest belt. Elevation 1950-2000 m. Annual precipitation 1500 mm. Period of activity for amphibians about five months, from early May to late September. Total number of studied specimens 22: 21 adult males, 1 adult female.

(5) Surroundings of the Mamisoni Mountain Pass in Racha Province, the central part of the Great Caucasus, southern slopes. Alpine meadows. Elevation 2550 m. Annual precipitation 1500 mm. Period of activity for amphibians about three months, from mid-May to the end of August. Total number of studied specimens 22: 21 adult males, 1 adult female.

Table I. - Climatic conditions of studied locations. E, elevation above sea level (meters); R, sum of sun radiation (ccal/cm²/year); TJA, mean temperature of January (°C); TJU, mean temperature of July (°C); DWP, duration of the period without freeze (days); SumT, sum of temperatures for the period with stable mean temperature above 5°C; AP, median annual precipitation (mm); DS, duration of the period of stable snow cover (days). BC, Borjomi Canyon; GV, Gujareti Village, subalpine belt; LT, Lake Tabatskuri, subalpine belt; DU, upstreams of the river Duruji, upper limit of forest belt; MP, Mamisoni Pass, Racha. Most of the data are based on the *Atlas of the Georgian SSR* (DJAVAKHISHVILI et al., 1964). Data on the annual precipitation are according to VLADIMIROV et al. (1991). For E, DWP, AP and DS, median values between minimal and maximal average estimations are given; for TJA, maximal average estimations; for R, TJU and SumT, minimal average estimations.

	E	R	TJA	TJU	DWP	SumT	AP	DS
BC	1000	135	-4	+18	137	3000	1000	88
GV	1900	>150	-8	+14	~100	2000	900	125
LT	2000	>150	-8	+12	~100	2000	1000	125
DU	1950	>150	-2	+20	137	3000	1700	125
MP	2550	>150	-10	+10	88	1500	1500	>150

Climatic conditions at these localities (according to DJAVAKHISHVILI et al, 1964) are shown in Table I.

Body length (L: snout-urostyle length) of each specimen was measured by sliding calipers with the distance between points 0.1 mm. The presence and brightness of the light mid-dorsal stripe was recorded as clear, unclear or absent. Age was estimated by standard skeletochronological methods (SMIRINA, 1989; CASTANET & SMIRINA, 1990).

For skeletochronology, femur (all frogs from Gujareti, Tabatskuri and Mamisoni Pass and 20 specimens from Borjomi Canyon) as well as second phalange of fourth toe of right foot (the remaining frogs from Borjomi Canyon) were used. Sections 25 μ thick were prepared with a cryostat, stained with Boemer hematoxylin and examined under a light microscope. The line of the first hibernation is usually resorbed, as in other species of brown frogs (LEDENTSOV, 1990). In most cases, age was estimated as N + 1, where N is the number of fully visible lines of arrested growth (LAGs). In frogs collected during early spring, the last LAG is invisible as well. In such cases, age was assumed as N + 2. The numbers of visible LAGs in phalanges and femurs of a specimen were always equal. Duplicated or additional LAGs, which can be observed sometimes on the sections of tubular bones of brown frogs together with true ones (e.g. SMIRINA, 1989; LEDENTSOV, 1990) were rare.

Statistical analysis of differences between samples in body length of frogs was conducted using the Student t test (ordinary method and modified method for small samples with different dispersions; ZAITSEV, 1984). Differences in age distribution were tested with a nonparametric Kolmogorov-Smirnov λ test. Differences in proportion of striped specimens in samples were tested with Fisher's angular method (ZAITSEV, 1984).

RESULTS

OCCURRENCE OF THE "STRIATA" PHENOTYPE

In Borjomi Canyon, only four of 138 examined frogs (2.9 %) had a bright mid-dorsal stripe, and 89 % had not even an unclear stripe. In Gujareti, 35 frogs (74 %) had a bright stripe and only 13 % were unstriped. Among frogs collected near Lake Tabatskuri, 77 % had a bright stripe and 11 % were unstriped. No obviously striped frogs were found in samples from Great Caucasus (Duruji Upstreams and Mamisoni Pass), though in each of these samples a few frogs with very unclear light stripe in the middle part of the back were found (Table II). Differences in the proportion of specimens with bright stripe are significant, not only between "striped" populations from Gujareti and Tabatskuri and all other populations ($P < 0.001$) but also between the population from Borjomi Canyon and the sample from Mamisoni Pass ($P < 0.01$). Therefore, in populations from the Trialeti Ridge an increase in the proportion of striped frogs with elevation was very clear, though it was not observed in the Great Caucasus.

BODY LENGTH OF ADULT FROGS

Frogs from Tabatskuri were characterized by the smallest body size (62-63 mm on average; Table II). Frogs from Duruji Upstreams were slightly larger: 62-66 mm. Body length of specimens from other localities showed no significant differences (though frogs from Mamisoni Pass were especially large). In Borjomi Canyon, females were significantly ($P < 0.01$) larger, in comparison with males. Mean body length of specimens from Borjomi Canyon, Gujareti and Mamisoni Pass varied from 67 to 73 mm. Differences between most of samples are significant (Table III).

AGE DISTRIBUTION OF ADULT FROGS

Age distributions of adult frogs are shown in Table IV. In sections of tubular bones of frogs from Trialeti Ridge (Borjomi Canyon, Gujareti, Tabatskuri), as well as from Duruji Upstreams, one to six LAGs were observed (fig. 2) suggesting that the ages of the animals are two to seven years. In the femur sections of frogs from Mamisoni Pass, from four to ten LAGs were seen (i.e., ages five to eleven years). The "youngest" population inhabits Lake Tabatskuri (mean age of adults 2.6-2.8 years). The mean age of frogs

Table II. - Morphological features of *R. macrocnemis* populations from different localities. S, percentage of frogs with clear stripe; PS, percentage of frogs with unclear stripe ("pseudostriata"); *N*, sample size; *M*, mean; *SE*, standard error. For other abbreviations, see Table I. For Borjomi Canyon, measurements of frogs collected during a five-year study (since 1989) are given.

	Coloration			Body length (mm)					
				♂			♀		
	N	S (%)	PS (%)	*N*	*M*	*SE*	*N*	*M*	*SE*
BC	138	3	8	216	67.1	0.34	88	69.3	0.73
GV	47	74	13	13	70.5	1.98	6	72.6	2.02
LT	63	77	12	27	62.7	0.87	13	62.3	1.09
DU	22	0	4	21	62.4	3.80	1	66.3	-
MP	117	0	4	96	72.3	0.70	20	73.1	1.02

Table III. - Significance of inter-sample differences in body length of *Rana macrocnemis*. Values of Student *t* are given as well as levels of significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. For other abbreviations, see Table I.

♂					♀			
	BC	GV	LT	UD		BC	GV	LT
GV	0.85				GV	1.54		
LT	*** 4.71	*** 4.50			LT	*** 5.33	*** 5.53	
UD	1.94	1.89	0.08					
MP	*** 6.68	0.86	*** 8.59	*** 4.63	MP	* 2.42	0.28	*** 6.40

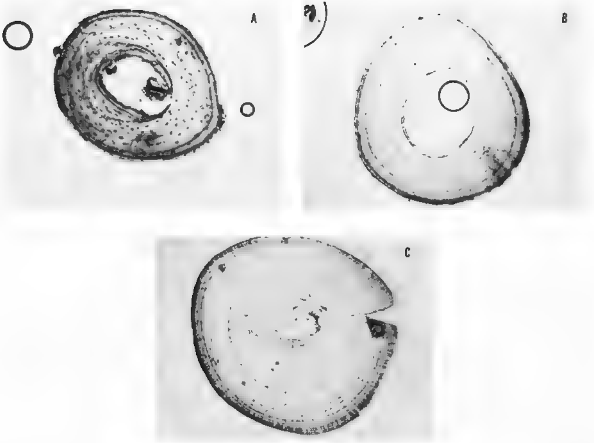


Fig. 2. – Femur sections of *R. macrocnemis* from different populations. A, Borjomi Canyon, female, three full LAGs (four years of age); B, Gujareti Village, female, three full LAGs (four years of age), C, Mamisoni Pass, male, eight full LAGs (nine years of age).

Table IV. - Age distribution of *Rana macrocnemis* from different localities. *N*, sample size; MA, mean age in years; *SE*, standard error. For other abbreviations, see Table I. Percentage of frogs of different age classes is indicated.

		N	MA	*SE*	Age in years (%)									
					2	3	4	5	6	7	8	9	10	11
BC	♂	92	2.95	0.10	36	45	11	8	1					
	♀	30	3.60	0.22	17	33	33	10	3	3				
GV	♂	13	3.39	0.31	8	69	15			8				
	♀	6	3.50	0.22		50	50							
LT	♂	27	2.63	0.14	52	33	15							
	♀	13	2.84	0.18	31	54	15							
DU	♂	21	3.57	0.68	5	38	52	5						
	♀	1	4.00	-			100							
MP	♂	76	7.75	0.33				8	13	21	31	14	8	5
	♀	19	7.47	-				10	16	21	27	21	5	

Table V. - Significance of inter-sample differences in age distribution of *Rana macrocnemis*, using Kolmogorov-Smirnov λ test. For abbreviations, see Tables I and III.

♂					♀			
	BC	GV	LT	UD		BC	GV	LT
GV	0.93				GV	0.38		
LT	0.73	1.30			LT	1.05	0.71	
UD	1.54*	0.96	1.61*					
MP	6.45***	3.06***	4.46***	3.98***	MP	3.21***	2.14***	2.78***

Table VI. - Index of absolute growth rate ($IG = L \times MA^{-1}$) and weighted index ($TIG = IG \times \Sigma t^{-1} \times 1000$, where t is the sum of effective temperatures for the warm period: average twenty-four-hour temperature + 5°C and more) for different populations of *Rana macrocnemis*. For abbreviations, see Tables I and III.

	BC		GV		LT		DU		MP	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
IG	22.74	19.25	20.80	20.74	23.84	21.9	17.48	16.58	9.01	8.04
TIG	7.6	6.4	10.4	10.4	11.9	11.0	5.8	5.5	6.0	5.4

inhabiting Borjomi Canyon, Gujareti and Duruji Upstreams varied from 3.2 to 4.2 years, but the mean age of frogs from Mamisoni was much higher and reached about eight years. Differences in the age distributions of frogs from Mamisoni Pass, on the one hand, and all other populations, on the other, are significant. Frogs from Duruji Upstreams are significantly older than those from Borjomi Canyon (Table V). In all localities females were slightly older than males, but differences are significant only for Borjomi Canyon ($P < 0.05$).

Post-metamorphic growth rates

The ratio $IG = L \times MA^{-1}$ of mean body size of adults (L, mm) to their mean age (MA, years) can be assumed to be a good index of absolute growth rate. This index varied between 19 and 24 in animals from Borjomi Canyon, Gujareti and Tabatskuri; it was less (about 17) in Duruji Upstreams, and did not exceed 9 at Mamisoni Pass. No differences in the growth rates of the sexes were detected.

Obviously, growth rates depend on the climatic conditions of the location. We cannot detect genetic interpopulation differences in growth rates based only on observed growth rates, but we have to take into account climatic differences between locations. Sum of temperatures for the activity period of frogs (which more or less coincides with the period when stable temperature exceeds 5°C), seems to be the most important quantitative climatic variable affecting the growth rates of frogs. The modified index of growth, more available for interpopulation comparisons than IG, was calculated in the following manner: $TIG = IG \times \Sigma t^{-1} \times 1000$, where t represents the sum of temperatures for the activity period. Calculated values are given in Table VI. Judging from estimated values of TIG, similarity between different populations where unstriped frogs predominated (Duruji Upstreams, Mamisoni Pass and Borjomi Canyon) was higher than between any of these populations and populations with striped frogs (Gujareti and Tabatskuri).

DISCUSSION

Despite previous studies (see Introduction), the *Rana macrocnemis* complex remains poorly known and more work is needed before a clear taxonomy of this group can be proposed. Pending such studies, we here adopt a conservative attitude, and we use for the Caucasian brown frogs the oldest available name for frogs of this complex, i.e. *Rana macrocnemis* Boulenger, 1885.

Taking into consideration the great intra-population variability in all three localities from Trialeti Ridge (Borjomi Canyon, Gujareti Village and Lake Tabatskuri), as well as the free interbreeding that occurs between different phenotypes, we could unify them in the same metapopulation system ("Trialeti"). The most important question appears to be why there is such marked morphological differences between different populations within this system.

At the intraspecific level, growth rates of specimens are related to two main factors: climatic conditions at the locality and genetically determined growth rates. Moreover, actual growth rate of each individual depends on the attained body size: growth slows down in animals reaching definitive species-specific size. Populations from Trialeti Ridge differed one from another in each of these three characteristics. Borjomi Canyon, situated at an elevation of about 1000 m in a forested gorge, is characterized by a relatively mild climate (sum of effective temperatures about 3000, January temperature −4°C, etc.; see Table I) in comparison with the other two localities. Attained body size is especially small in the population at Lake Tabatskuri. At the same time, judging from the proportion of striped frogs, the genetic composition of populations from Gujareti and Lake Tabatskuri clearly differ from that of the population at Borjomi Canyon (though the distance between populations from Borjomi Canyon and Gujareti is less than 18 km and the only natural barrier between them is a small ridge of about 2000 m maximum elevation).

We considered the role of climatic conditions and weighted the indices of growth rates according to the sum of effective temperatures (reflecting the period of activity of frogs) at different elevations. Weighted growth index was especially high for frogs inhabiting the vicinity of Lake Tabatskuri. This may have resulted in especially early maturation, at the expense of decreased mean adult body size, in this population. However, frogs from Gujareti, which mature at the same age and the same body size as frogs from Borjomi Canyon, also grow much more rapidly than frogs from the latter locality. Thus, we propose that post-metamorphic growth rates for Trialeti metapopulation are due to genetic differences between local populations, reflected in the different frequencies of striped specimens. The growth index of frogs from the populations where striped animals predominate is about 1.5 times more than in the "unstriped" population inhabiting Borjomi Canyon. Accelerated growth in the mountain populations of Trialeti Ridge has an adaptive value. If frogs from Gujareti had the same growth index as in the Borjomi Canyon, they would mature 1.5 times later (taking into account differences in the period of activity and sum of effective temperatures). If mean age of females from the Borjomi Canyon reaches 3.6 years, in Gujareti it would reach about 5.4 years.

Intrinsic growth rate of a population, in accordance with well-known demographic models (e.g. WILLIAMSON, 1972), is described by the equation $\sqrt[\tau]{b - d + 1} = \sqrt[\tau]{\lambda}$, where b is the mean value of fecundity, d the mean mortality rate for adult animals and τ the mean age of adult frogs. If the animals from two populations have the same fecundity and mortality rates, the ratio of their productivities would be $k = \lambda^{(1/\tau 1 - 1/\tau 2)}$, where τ_1 and τ_2 are the mean ages of animals in populations where animals mature at a younger and older age, respectively.

Genetically fixed rapid growth of frogs from Gujareti prevents displacement of local genotypes by the genotypes predominating in Borjomi Canyon, in spite of the latter breeding in more favourable climatic conditions

Frogs from Lake Tabatskuri grow and mature even faster than in Gujareti. If fecundity and mortality of these two populations were equal, the reproductive success of frogs inhabiting the surroundings of Tabatskuri would be higher. However, the fecundity of females with a body length of about six centimeters (mean size in Tabatskuri population) is 1.5 times lower than that of females of the same species with a body length of seven centimeters (TARKHNISHVILI, 1993). The small size of frogs inhabiting surroundings of Tabatskuri is probably the cost of advantages associated with rapid maturation. The productivities of frogs from different populations on Trialeti Ridge appear to be similar. This allows the stable coexistence of populations dominated by different morphs without the displacement of morphological characters as a result of interbreeding.

The results presented in this study enable the high proportion of striped specimens in some populations to be explained. However, the inverse situation, the very low proportion of striped frogs in Borjomi Canyon, remains to be explained. The hypothesis that in forested canyons selective pressure works against striped frogs cannot be excluded. In particular, it may be connected with the very unstable breeding sites in this habitat (see TARKHNISHVILI, 1993), taking into account the longer larval period of genetically striped brown frogs, demonstrated in *Rana arvalis* (ISHCHENKO & SHCHUPAK, 1974). However, this question requires further study.

In both populations from Great Caucasus, frogs with a bright stripe are absent, independently of the elevation and the climatic conditions. Overall, the climate in the Great Caucasus is more humid and mild, in comparison with Caucasus Minor localities situated at the same elevations (Table I): the sum of effective temperatures in the upper reaches of streams in Duruji (elevation 1900 m) is similar to that in Borjomi Canyon (1000 m). At the same time, the growth rates of frogs from this population are slightly lower than those of unstriped frogs from Borjomi Canyon and markedly lower than in "striped" populations from Gujareti Village and Lake Tabatskuri. The growth rates of frogs from Mamisoni Pass are lowest; even the growth index (TIG), which takes into account the coldest climate in this locality (Table I), shows a low value (Table IV). As a result, the actual productivity of frogs from Great Caucasus clearly declines with elevation. The only reason that can be hypothesized for this situation is an absence of a genotype, correlated with rapid growth, in the gene pool of the metapopulation of brown frogs inhabiting Great Caucasus.

An interesting conclusion can be outlined. In spite of the high external similarity between populations from Borjomi Canyon and Great Caucasus, they belong to different

metapopulation systems. The first system (western part of the Trialeti Ridge) includes genotypes connected with rapid growth. This facilitates the rapid redistribution of genotypes when the population is exposed to new climatic conditions and the appearance of specific "mountainous" populations, composed almost exclusively of striped frogs. In the gene pool of the second system (southern slopes of Great Caucasus) such genotypes are simply absent.

In *R. macrocnemis* populations from Armenia, inhabiting elevations of 1900-3000 m, frogs of one to three years of age predominate (LEDENTSOV & MELKUMYAN, 1986). The situation is similar to that in localities from Trialeti Ridge, which belong to the same mountain system of Caucasus Minor.

This point of view requires further studies. Expected difficulties could be outlined. For instance, the presence of striped frogs in the population does not necessarily prove the presence of the genotype "striata" in its gene pool, because under changed developmental conditions they can appear even in the descendants of genetically unstriped parents.

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Use of terrestrial habitats by amphibians in the sandhill uplands of north-central Florida

C. Kenneth Dodd, Jr.

National Biological Service, 7920 N.W. 71st Street, Gainesville, Florida 32653, U.S.A.
kdodd@nervm nerdc.ufl.edu

A total of 506 individuals of 12 amphibian species was captured during sampling of two upland communities in north-central Florida, USA, in 1989 and 1990. Amphibians were found as far as 914 meters from the nearest water body, although the actual breeding site could have been farther away. Of the species dependent on water for breeding, three (*Bufo terrestris, Gastrophryne carolinensis, Scaphiopus holbrooki*) accounted for 87 % of the amphibians captured. No significant correlation was found between the total number of amphibians captured per trap and trap distance to nearest water body. Most amphibians (83 %) were caught less than 600 meters from the nearest water. Upland communities appear to be used extensively by certain amphibians, especially terrestrial burrow users. As such, management programs need to be expanded to include surrounding uplands if amphibian declines are to be prevented.

Introduction

For amphibians that rely on water for reproduction, the vast majority of field studies center on activities at or near breeding sites (e.g., references in Duellman & Trueb, 1985). Amphibians are conspicuous at breeding locations as males call to attract females and establish territories, amplectant pairs mate and deposit eggs, larvae grow and either metamorphose or become neotenes, and adults and metamorphosed young begin to disperse to uplands or other habitats used during non-reproductive times of the year.

The life history of wetland-breeding amphibians away from breeding sites is poorly understood. It seems generally accepted that individuals may disperse some distance from breeding sites, perhaps varying among species, life stages, or in response to quality and availability of adjacent habitats. At least one text, however, terms distances moved into adjacent habitats as "minor" (Zug, 1993). Except for a few studies (e.g., Pearson, 1955; Williams, 1973; Semlitsch, 1981), the presence of water-breeding amphibians in uplands has been inadequately documented in the North American literature, and then often on the basis of a single or relatively few observations on a few species (Table I). The distances that most species in the southeastern United States can or normally disperse are unknown.

Table I. - Examples of distances that North American amphibians have been recorded moving overland under natural conditions. Movements along watercourses and terrestrial movements associated with displacement experiments are not included. *M*, mean.

Species	Location	Movement	Reference
Salamanders			
Ambystoma californiense	California	120 m	HOLLAND et al. (1990)
Ambystoma californiense	California	1600 m[1]	AUSTIN & SHAFFER (1992)
Ambystoma jeffersonianum	Kentucky	*M* = 250 m	DOUGLAS & MONROE (1981)
Ambystoma jeffersonianum	Indiana	*M* = 252 m (20-625 m)	WILLIAMS (1973)
Ambystoma jeffersonianum	Indiana	*M* = 92 m (3-247 m)[1]	WILLIAMS (1973)
Ambystoma jeffersonianum	Michigan	152 m	WACASEY (1961)
Ambystoma jeffersonianum	New York	1610 m	BISHOP (1941)
Ambystoma macrodactylum	California	30 m	STEBBINS (1951)
Ambystoma maculatum	North Carolina	18-823 m	GORDON (1968)
Ambystoma maculatum	Michigan	*M* = 192 m (157-249 m)	KLEEBERGER & WERNER (1983)
Ambystoma maculatum	Kentucky	*M* = 150 m (6-220 m)	DOUGLAS & MONROE (1981)
Ambystoma maculatum	Missouri	*M* = 150 m (to 172 m)	SEXTON et al. (1986)
Ambystoma maculatum	New York	75 m	WILSON (1976)
Ambystoma maculatum	Indiana	*M* = 64 m (0-125 m)	WILLIAMS (1973)
Ambystoma opacum	Indiana	*M* = 193 m (0-450 m)	WILLIAMS (1973)
Ambystoma talpoideum	South Carolina	81-261 m	SEMLITSCH (1981)
Ambystoma texanum	Indiana	*M* = 52 m (0-125 m)	WILLIAMS (1973)
Ambystoma tigrinum	South Carolina	162 m	SEMLITSCH (1983)
Notophthalmus viridescens	Massachusetts	800 m	HEALY (1975)
Frogs			
Acris crepitans	Texas	167 m	PYBURN (1958)
Acris gryllus	Florida	823 m	CARR (1940)
Acris gryllus	Kansas	183 m	FITCH (1958)
Bufo americanus	Minnesota	1000 m	EWERT (1969)
Bufo americanus	Ontario	594 m	OLDHAM (1966)
Bufo cognatus	Minnesota	300-1300 m	EWERT (1969)
Bufo hemiophrys	Minnesota	25 m	OLDFIELD & MORIARTY (1994)
Bufo hemiophrys	Minnesota	61 m	BRECKENRIDGE & TESTER (1961)
Bufo woodhousei	Kansas	579 m	FITCH (1958)
Gastrophryne olivacea	Kansas	to 183 m	FITCH (1956)
Pseudacris nigrita	Kansas	183 m[1]	FITCH (1958)
Pseudacris regilla	Oregon	237 m[1]	JAMESON (1956)
Pseudacris triseriata	Indiana	100 m[2]	KRAMER (1974)
Rana capito	Florida	1600 m	CARR (1940)
Rana capito	Florida	2000 m	FRANZ et al (1988)
Rana catesbeiana	New York	76 m	INGRAM & RANEY (1943)
Rana catesbeiana	New York	107 m	RANEY (1940)
Rana palustris	Minnesota	500 m	OLDFIELD & MORIARTY (1994)
Rana pipiens	Minnesota	1500 m	OLDFIELD & MORIARTY (1994)
Scaphiopus bombifrons	Kansas	914 m	FITCH (1958)
Scaphiopus holbrooki	Florida	402 m	PEARSON (1955)

[1] Represents juvenile dispersion.
[2] Estimated from map.

In 1989 and 1990, DODD & FRANZ (1995) conducted an inventory of the snake community inhabiting upland sites on the Katharine Ordway Preserve in north-central Florida. During the course of the survey, substantial numbers of amphibians were captured in wire mesh funnel traps. Inasmuch as little information was available on the presence of amphibians in these physically harsh environments, I tabulated capture results to determine which species used upland habitats and how far they were from the nearest potential breeding site. Although the original study was not designed to survey the amphibian community, these data may be helpful in planning future research and in directing attention to the importance of uplands in the conservation of amphibian populations that depend upon isolated wetlands for breeding.

STUDY SITE AND METHODS

The Katharine Ordway Preserve-Swisher Memorial Sanctuary is a 3750-ha tract located approximately 5 km SE of Melrose, Putnam County, Florida. This upland sandhill region lies within the Interlachen Karstic Highland at the southern end of Trail Ridge. The area represents a portion of a dune complex that probably formed in association with active beach development during periods of higher sea levels (WHITE, 1970). The dunes have been secondarily modified by solution activities in the underlying limestone to form sinkholes and karst basins. Many of these solution features hold water to form ponds, lakes, and wetlands. More than 70 water bodies exist on the property. There are 27 species of amphibians recorded from the Ordway Preserve (FRANZ, 1995), and at least 16 species have been recorded in a single small temporary pond in upland habitat (DODD, 1992).

Two of the eight vegetative communities known from the Ordway Preserve (FRANZ & HALL, 1991) were sampled during this study. Both upland communities, high pine forest and sand live oak hammock, have been influenced by human disturbance and past fire histories Also known as "sandhill", high pine forest is dominated by longleaf pine (*Pinus palustris*), turkey oak (*Quercus laevis*), and wiregrass (*Aristida stricta*). The community occurs on deep sands associated with dune ridges. Sand live oak hammock occurs as fringes around certain wetland types and on ruderal sites. Dominated by sand live oak (*Q. geminata*) and occasionally by laurel oak (*Q. hemisphaerica*), sand live oak hammocks can have dense understories composed of sapling oaks, blueberries (*Vaccinium* spp.), myrtle oak (*Q. myrtifolia*), and other woody plants. Reindeer lichens (*Cladonia* spp. and *Cladina* spp.) and herbaceous species are more prevalent in open hammocks without a dense understory. General information and references on these and other Florida communities are in MYERS & EWEL (1990).

Between 15 and 25 % of the property is believed to have been cleared for agriculture and human habitation since 1850 (R. FRANZ, personal communication). Several of these areas have undergone succession to xeric sand live oak hammocks. Regular prescribed burning of high pine forests was established in 1983 as a part of the Ordway Preserve's management plan for reestablishing the native longleaf pine ecosystem. Summer air temperatures in upland habitats routinely approach 36°C, and substrate temperatures of 50°C have been recorded. The porous sandy soils dry rapidly at and immediately below

the surface. A combination of poor soil moisture retention and high temperatures at or near the substrate surface make these upland sandhill habitats potentially harsh for small amphibians.

In 1989, 100 individually numbered screen wire mesh double-opening funnel traps (90 cm long by 18 to 25 cm diameter) were placed at six upland sites as follows: 31 traps in closed xeric (sand live oak) hammock; 59 traps in sandhill (high pine) habitat; and 10 traps in open xeric (sand live oak) hammock. Exact locations of the traps and descriptions of the habitats are presented elsewhere (DODD & FRANZ, 1995).

Most traps were set along fallen trees and branches that formed natural drift fences. At certain locations, traps were set along drift fences made of 10 m sections of galvanized metal set in 4-pronged arrays (see figure 1 in CAMPBELL & CHRISTMAN, 1982, and figure 11A in CORN, 1994). All traps were covered with palmetto fronds to prevent captured animals from overheating in the direct sun and to provide cover. In 1989, traps were checked daily from April 4 through November 17 (23,800 trap nights) between 07.00 and 12.00 h. Species identifications were recorded and animals were released in cover within several meters of the trap.

In 1990, the same areas were resampled using the same general techniques except that all sites were not sampled simultaneously. In addition, 30 traps were set in closed xeric hammock habitat in the vicinity of a temporary pond (Breezeway Pond). Traps were placed in the same positions as in 1989. From 20 to 30 traps were checked daily from April 4 to September 27. The dates when individual sites were sampled are provided in DODD & FRANZ (1995). This protocol resulted in a sampling period of 4,490 trap nights.

The location of each trap (excluding the Breezeway Pond traps) was plotted on aerial photographs, and the distance to the nearest potential source of water for breeding by amphibians was measured to the nearest meter. I examined possible effects of trap placement on amphibian capture in relation to habitat (sandhill, live oak hammock with open understory, live oak hammock with dense understory), type of water body (lake versus pond), and specific water body. Ponds had surface areas less than 4 ha and usually dried during droughts. Although Smith Lake dried during the intense drought of the late 1980's to early 1990's, the other lakes were permanent. Inasmuch as the data were not normally distributed, most comparisons were made using the nonparametric Kruskal-Wallis test (procedure NPAR1WAY, ANONYMOUS, 1988). The effect of trap distance from nearest water body on the total number of amphibians captured was examined using Spearman rank correlation. *Eleutherodactylus planirostris* has terrestrial development and therefore was excluded from analyses of the relationship between trap distance and nearest water body. Statistical analyses were performed using the SAS program for microcomputers (ANONYMOUS, 1988) and ABSTAT version 4 (ANONYMOUS, 1987). The level of significance was set at $\alpha = 0.05$.

RESULTS

A total of 506 amphibians comprising 12 species was captured during trapping for snakes (0.2 amphibians/trap night in 1989, 0.1 amphibians/trap night in 1990). Amphib-

ians were found in funnel traps at distances from 42 m to 914 m from the nearest water (Table II). Individuals were found in 90 different traps; there was no significant difference in mean distance (MD) to nearest water body between funnel traps in which amphibians were caught (MD = 427.9 m) and those in which amphibians were not caught (MD = 334.5 m) (χ^2 = 3.05, 1 *DF*, *P* = 0.08).

Trapping location was not random with respect to water bodies. The mean distance from traps to the nearest water body varied significantly among different ponds and lakes (Table III; χ^2 = 69.4, 5 *DF*, *P* = 0.0001) and in relation to water body type (lakes, MD = 495 m, *N* = 57 traps; ponds, MD = 312 m, *N* = 33 traps; χ^2 = 18.8, 1 *DF*, *P* = 0.0001). Perhaps because of these potential trap biases, there was no significant correlation between the total number of amphibians captured per trap and the distance to nearest water body (fig. 1; r_s = 0.3084, *P* > 0.05, *N* = 100). Likewise, there was no significant difference in the mean distance to nearest water body among the traps in different habitat types (Table IV; χ^2 = 3.3, 2 *DF*, *P* = 0.19).

Only 28 % of the amphibians captured were in traps less than 400 m from the nearest wetland, although 51 % of the traps were less than 400 m from the nearest water body. As distance increased to 500 m (accounting for 77 % of the traps), the amphibian capture percentage increased to 67.6 %, and at 600 m (accounting for 88 % of the traps) the percentage increased to 82.9 %. Few specimens (11) were captured from 600 to 800 m (9 % of the traps), or at distances greater than 900 m (14 amphibians and 2 % of the traps) However, 11.6 % of all captures were recorded from 800 to 900 m; these traps accounted for only 4 % of the trapping effort. Capture was not random with respect to habitat type. More amphibians were captured in open xeric habitat, and less in closed xeric hammock, than might be expected if the number of amphibians captured among habitats was in direct proportion to trapping effort (χ^2 = 10 73, 2 *DF*, *P* = 0.0047) (Table IV).

Discussion

Trap biases exist in the survey protocol, and a rigorous assessment needs to be made concerning factors that influence amphibian presence in upland communities. However, these results suggest that the presence of amphibians in southeastern upland habitats may be more significant than is usually recognized, especially by land and resource managers, and that amphibians occupy habitats even at considerable distances from the nearest potential breeding site. Amphibians captured during the inventory may have bred in more distant wetlands than the nearest wetland to the trap in which they were captured. Therefore, the maximum distances shown in Table II should not be confused with the maximum distances that amphibians are capable of traveling. Likewise, the data in Table IV should not be inferred to mean that amphibians prefer closed xeric hammock to the other habitat types in Florida uplands. These data do suggest avenues for potential research, however.

Although the data are not amenable to analysis of species' preferences because of the biased sampling protocol, it appears that burrow-using terrestrial frogs (toads, spadefoots, narrow-mouthed toads) are more likely than the more arboreal and aquatic species (hylids

Table II. - Species collected and distances (m) from nearest water body for amphibians captured during funnel trapping in upland habitats of north-central Florida, 1989 - 1990. *SD*, standard deviation.

Species	Total number captured	Mean ± *SD* (range)
Acris gryllus	7	383 ± 81.4 (255-492)
Bufo quercicus	15	574 ± 216.8 (404-914)
Bufo terrestris	54	515 ± 202.2 (46-914)
Eleutherodactylus planirostris[1]	91	478 ± 136.7 (46-895)
Gastrophryne carolinensis	162	420 ± 216.8 (42-914)
Hyla cinerea	6	545 ± 181.1 (457-914)
Hyla femoralis	6	266 ± 317.5 (42-815)
Hyla squirella	5	594 ± 188.3 (446-914)
Notophthalmus perstriatus	12	225 ± 180.2 (42-709)
Pseudacris ocularis	1	434
Rana utricularia	1	95
Scaphiopus holbrooki	145	539 ± 211.2 (95-914)

[1] Has terrestrial development.

Table III. - Trap distances (m) in relation to nearest water body on the Ordway Preserve. *SD*, standard deviation.

Name	Wetland type	Number of traps	Mean ± *SD* (range)	Number of amphibians (%)
Blue	Pond	8	461 ± 40.1 (392-511)	15 (3.5)
Enslow	Lake	20	322 ± 46.7 (244-396)	31 (7.2)
Goose	Lake	10	825 ± 75.0 (709-914)	76 (17.8)
One-Shot	Pond	30	264 ± 122.7 (42-469)	91 (21.3)
Ross	Lake	22	501 ± 53.3 (419-610)	180 (42.2)
Smith	Lake	10	420 ± 56.7 (373-533)	64 (15.0)

Table IV. - Amphibian captures in relation to habitat type and trap effort. Data for 1989 captures. *SD*, standard deviation.

Habitat	Number of traps	Distance (m) to water: mean ± *SD* (range)	Number of amphibians (% of capture)
Sandhills	59	432.8 ± 229.5 (41.9-914.4)	248 (58 %)
Closed Xeric Hammock	31	403.0 ± 109.6 (243.8-579.1)	95 (22 %)
Open Xeric Hammock	10	469.0 ± 31.5 (419.1-499.0)	83 (19 %)

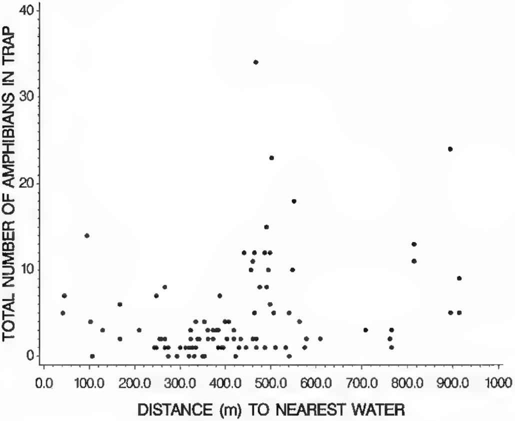


Fig. 1. — The relationship between the total number of amphibians captured in funnel traps and the distance of the funnel trap to the nearest potential breeding site.

and ranids) to be captured by randomly placed terrestrial traps. Arboreal species travel well into uplands in dense oak hammocks surrounding lakes on the Ordway Preserve, but they appear to travel through the tree canopy rather than on the ground (R. BOUGHTON, personal communication). Ranids are also known to make extensive overland movements in Florida uplands (e.g , FRANZ et al., 1988), but their travel routes, time and duration of travel, and susceptibility to trapping are poorly understood.

In upland Florida habitats, amphibians are found in burrows of other animals such as lizards (e.g., *Gastrophryne carolinensis* in the burrows of *Cnemidophorus sexlineatus*), pocket gophers (*Geomys* sp.), and gopher tortoises (*Gopherus polyphemus*), under logs and other surface debris, and in tree cavities (personal observation). Gopher tortoise burrows, in particular, are excellent retreat sites, with nine amphibian species recorded from them (JACKSON & MILSTREY, 1989). The extensive collection of amphibians in funnel traps suggests that these animals are not sedentary but instead leave burrows and other cover sites and move around.

Most North American amphibian field studies involving wetland-breeding species are centered around the breeding site. Such a bias is akin to studying sea turtles only on a nesting beach. Both amphibians and sea turtles spend a great majority of their lives away from the habitats most easily studied by researchers. Just as sea turtle biologists have gained new insights into the life histories of turtles by developing methodologies that allow them to investigate activity away from nesting beaches, amphibian biologists must adopt research methods that begin to probe an amphibian's life away from the breeding pond (DENTON & BEEBEE, 1992; HEYER et al., 1994). Few researchers have conducted field studies of amphibians away from the breeding site (e.g., PEARSON, 1955; DENTON & BEEBEE, 1993; PASANEN et al., 1993; LOMAN, 1994). However, such studies have allowed investigators to take a more holistic view of the ecological requirements and activities of a species.

There has been great concern for the status of amphibian populations and species throughout the world (WAKE et al , 1991; BLAUSTEIN, 1994, BLAUSTEIN et al., 1994). Declines have been reported in a variety of habitats and often have involved wetland-breeding species. Few studies, however, have assessed habitat requirements away from breeding sites. Biologists conducting inventories of upland communities should routinely note the distances to nearest wetlands if wetland-breeding amphibians are found.

Management guidelines that promote wetland protection in order to conserve amphibians yet ignore non-breeding upland habitats (e.g., WILSON, 1994) are destined to failure if resident animals move far from ponds and other wetlands. Buffer zones need to be established around breeding ponds to ensure survival of the amphibian community. In this regard, 82.9 % of the amphibians I captured were within 600 m of the nearest breeding site, although I could not determine if this distance would be effective at protecting the local amphibian community because of the study's sampling biases. DUBOIS (1991: 396) suggested that in tropical regions protection of a buffer zone of 100 to 500 m along each side of watercourses would help conserving a large proportion of the batrachofauna. The need for buffer zones to protect wetland-resident turtle populations has also been recognized (BURKE & GIBBONS, 1995; K. BUHLMANN, personal communication).

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